

Atopsyche mexicana (Banks), n. comb.

Philopotamus mexicanus Banks, Trans. Amer. Ent. Soc. 27: 370. 1901.

The type, in the Museum of Comparative Zoology, was examined in 1951 and found to be without abdomen, so that it is not possible at present to identify the specimen beyond genus.

The venation indicates definitely that it belongs to *Atopsyche*.

Atopsyche callosa (Navas)

I had an opportunity to study the type in the Paris Museum. Although labeled and recorded in the original description as a male, the specimen actually is a female, and could not be identified except to genus.

ORNITHOLOGY.—*Feeding adaptations and systematics in the avian order Piciformes*. WILLIAM J. BEECHER, Chicago Natural History Museum. (Communicated by Herbert Friedmann.)

Recently Dr. Herbert Friedmann offered for my study some spirit specimens of honeyguides (Indicatoridae), together with other members of the order Piciformes. It was hoped that such an investigation as I carried out for the Neotropical honeycreepers (Beecher, 1952) might cast further light on both the feeding adaptation and systematic position of these birds so well studied by Friedmann (in MS.). Checking the systematic position of the honeyguides required a somewhat hasty completion of a long-time survey of jaw musculature in the class Aves which I will publish elsewhere. The present paper simply deals with the food adaptations in the head region of the piciform honeyguides, barbets, puffbirds, jacamars, toucans, and woodpeckers, which seem to occupy an interesting position between the perching birds (Passeriformes) and the remaining avian orders. Specimens used are from the collections of the United States National Museum and Chicago Natural History Museum. For their use or for advice, I am indebted to Herbert Friedmann, Austin L. Rand, Emmet R. Blake, and D. Dwight Davis.

SPECIMENS EXAMINED

Although a limited number of anatomical specimens was studied, the use of numerous skulls of related species considerably swells the list of material examined. This material is sufficient to suggest very strongly that the same constancy of muscle pattern found to hold for the species of passerine families holds for non-passerine families as well. Species dissected are: (Indicatoridae) *Indicator minor conirostris*, *I. exilis*, *I. maculatus*,

I. minor minor; (Ramphastidae) *Pteroglossus torquatus*, *Ramphastos cuvieri*, *Selenidera spectabilis*; (Capitonidae) *Lybius leucocephalus*, *Megalaema haemacephala*, *M. rafflesii*, *M. zeylanica*, *Trachyphonus purpuratus*; (Bucconidae) *Chelidoptera tenebrosa*; (Picidae) *Colaptes auratus*, *Dryocopus pubescens*, *Melanerpes carolinus*, *M. erythrocephalus*, *Piculus chrysochloros*, *Picumnus squamulatus*. No specimens of jacamars were on hand to dissect, unfortunately, but skulls strongly suggest their close alliance with the barbets.

INVESTIGATION TECHNIQUES

In undertaking this study I have pursued essentially the plan laid out in my paper mentioned above and in the more comprehensive work on the phylogeny of the Oscines (Beecher, 1953). This consists in comparing various systems throughout the groups considered, as illustrated in the figures for the families. In each of these the jaw musculature is illustrated in side view and oblique view (with eye removed), as indicated in black on the accompanying skull drawings. The tongue is drawn on the right above and the ectethmoid plate with its foramina (separating the orbital and nasal cavities), on the left. In the center is figured the horny palate pattern and the bill. The logic behind the comparison of systems is that it should be possible in an avian order to establish a ground plan from which the groups (families) are adaptively specialized. Special emphasis was placed on jaw muscle pattern as a family trait in the Oscines because song-bird families appear to be diverging from such a ground plan under the selection pressure of different food types and because each family tends to have a very constant pattern. In the present

order the muscle patterns seem to exhibit conservative differences between the families that prove ideal both for emphasizing their adaptive differences and at the same time encompassing them within the diagnosable ground plan of Piciformes. The other characters illustrated serve to safeguard against erroneously including a convergent species, occasionally possible if a single character is used blindly—and to further point up functional differences between the families in these less conservative parts. These systems will now be taken up below to see how well they support the current ornithological opinion that the piciform families are closely related and to show the extent to which they are differently adapted for food-getting.

THE JAW MUSCLE PATTERNS

No systematic account of muscle origins or insertions will be included here. This is well covered in Moller (1931) and Fiedler (1951); the abbreviated account in Beecher (1951b) should suffice for the understanding of muscle function stressed in the present paper since the same muscles are concerned.

A strong facies resemblance between the jaw muscle patterns of the piciform families persists through their quite different food adaptations, which constitutes one of the best arguments for close relationship. The far posterior position of the flattened pterygoid bones where they articulate with the palatines along the sphenoidal rostrum causes *M. pterygoideus dorsalis posterior* (*M3b* in Figs. 1 and 2) to be nearly obscured from view, suggesting relationship with Trogoniformes and Coraciiformes. *M. pterygoideus dorsalis anterior* (*M3a*) is correspondingly enlarged to make up the needed power for retracting the pterygoids, its broad insertion on the sphenoidal clasp, formed by the articulation of the palatines and pterygoids, covering *M. pterygoideus ventralis posterior* (*M4b*). The functional result is unusual emphasis on palate retraction in the kinetic bills of all of these families. Since this retraction is translated by the nasofrontal hinge into a downward drag on the upper mandible, the unusually heavy construction of this part is clearly functional in feeding. Along with this is a considerable emphasis on the adductors. In Capitonidae and Ramphastidae *M. pseudotemporalis profundus* (*M5*) is powerfully developed for dragging on the orbital process of the quadrate and rocking this important bone backward on its articulation

with the cranial part of the skull, initiating palate retraction and adduction of the upper mandible.

This emphasis on the palatine retractors and the adductors is about proportional to the mass of the bill in the several families studied. In Capitonidae, and particularly in *Lybius* with its stout, notched bill, *M. pterygoideus ventralis posterior* (*M4b*) originates all along the outer surface of the mandibular ramus posteriorly, as well as on the customary inner surface. This is also noted in Ramphastidae and Picidae in progressively lesser degree (the former with *M4a* and *b* fused) but not in Indicatoridae. The adductors are also most strongly stressed in the Capitonidae and Ramphastidae, the temporal slip of *M. adductor mandibulae externus superficialis* (*M7a*), particularly, showing a deep incursion to the dorsal midline of the skull posteriorly. This is not met with in the Oscines but is characteristic of the Suboscines and a vast majority of other avian orders.

The Picidae have a good expression of both palatine retractors and adductors but are outstanding for the extreme emphasis on the protractors of the mandibles, *M. depressor mandibulae* (*M1*) and *M. protractor quadrati* (*M2*). This is especially so in the latter, which originates over most of the area of the interorbital septum which (unlike most birds) is thoroughly ossified in woodpeckers to protect the brain and unusually ossified in the other piciform families. This arrangement, which is met in the piculets as well as in the more highly-adapted woodpeckers, is also found among passerines in the nuthatch *Sitta*. Its effectiveness in prying is evident, and it is seen (with *M2* less well expressed) in numerous species of prying birds (Beecher, 1950; 1951a and b); but in woodpeckers it probably serves as part of an interesting shock absorbing mechanism. I disagree with Burt (1930) that the woodpecker bill is immovably joined to the skull in even the most highly adapted forms. The only unkinetic bird skull is seen in the lizard-like subclass Archaeornithes. In all other birds the upper mandible joins the skull at the naso-frontal hinge and the jugal-palatoptyergoid armature joins its base to the quadrate in a frame that slides along the sphenoidal rostrum under the control of the jaw musculature. The key bone in this process is the movable quadrate which permits these antero-posterior movements of the armature to be translated into elevating and depressing movements of the upper mandible

HONEY GUIDE ~ *Indicator minor* ~ INDICATORIDÆ

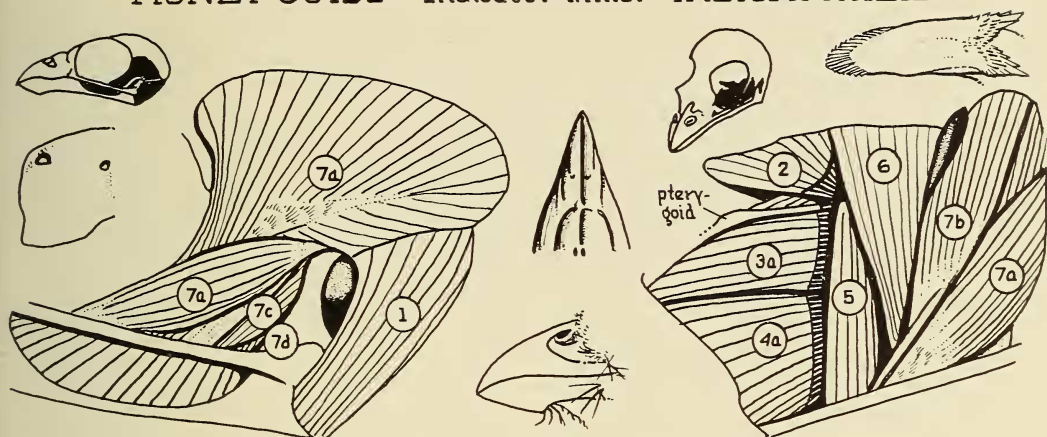


FIG. 1.—Detail drawing of jaw muscle pattern of the honeyguide (*Indicatoridae*).
Protractors. 1 depresses the lower mandible; 2 elevates the upper mandible.

- 1. *M. depressor mandibulae*
- 2. *M. protractor quadrati*
- Palatine retractors*. Combined action draws upper mandible downward.
- 3. *M. pterygoideus dorsalis*: a) anterior; b) posterior (underlies 2)
- 4. *M. pterygoideus ventralis*: a) anterior; b) posterior (underlies a)
- 5. *M. pseudotemporalis profundus*
- Mandibular adductors*. Combined action draws lower mandible upward.
- 6. *M. pseudotemporalis superficialis*
- 7. *M. adductor mandibulae*: a) *externus superficialis*; b) *externus medialis*; c) *externus profundus*; d) posterior

In the shock-absorbing mechanism of woodpeckers and nuthatches the antagonistic action of the enormous *M2* against the retraction of the pterygoid musculature probably holds the bill in a state of resilient rigidity as it rains its blows on a tree trunk. Woodpeckers also have a special nasal mucous gland (Technau, 1936); this is visible in the floor of the orbit just ventral to the ectethmoid plate and is less well expressed in sapsuckers (*Sphyrapicus*) than other genera. Since this may serve to trap dust raised by pecking (an occupational hazard of woodpeckers like silicosis among humans!) sapsuckers, habitually working soft, green wood, may not need it so much. This has nothing to do with the enormous sub-lingual mucous gland which serves to make the woodpecker tongue sticky.

The Indicatoridae, strange to say, show no specializations of the jaw musculature or salivary glands at all. The bill, too, is more generalized than that possessed by any other piciform family, except for the unusual feature that the tips of the peculiarly blunted mandibles meet without notable overlap of the upper—an adaptation, possibly, for biting off bits of wax and honey. But the general facies of the order is recognizable in the jaw muscle pattern which is more gen-

eralized than in any of the other families. This is clearly seen in the simple *M. pseudotemporalis superficialis* (*Mⁱ*) which, in the other families, shows a slight approach to the Suboscines and to Coraciiformes and possibly Trogoniformes. The honey-guide musculature is, in fact, the nearest seen in any of these families to the ideal ground plan for the order. This is not to state that this family is actually ancestral to the others but only that it may more nearly resemble the less specialized common ancestor. In other respects I am inclined to think the basic stock might have been more like the barbets but these have now, in process of developing a massive musculature for power, sheathed much of the musculature in tough aponeuroses to which shorter fibers fuse in semblance to the pinnate muscles so important in the higher Oscines. This is an arrangement found in primitive oscine shrikes like Craetidae, Prionopidae and Vangidae. The only muscles that could class as pinnate in Piciformes are the temporal slip of *M7a* and *M7c*. This supports the general opinion as expressed in Wetmore (1940; 1952) and in Mayr and Amadon (1951) that the group is somewhat more primitive than Passeriformes.

THE TONGUE

The tongue is not generally a very reliable index of relationship in birds (Beecher, 1951a) because it is apparently so readily modified in conjunction with an extreme feeding adaptation. This is true in Piciformes. The tongues of barbets are the generalized tongues of insect eaters, not distinguishable by any reliable characters from those of some passerine insect eaters, except that, like the other piciform families, the papillae of the posterior surface of the tongue are unusually abundant. The moderately frayed out horny tip is unspecialized in barbets and the tongues of honey eaters are very similar. The tongues of the toucans are simply elongate and narrow, with the fringe extending well posterior; such a tongue would be useful in lapping juice from pulpy fruits as well as in the usual process of biting out pieces. The woodpecker tongue is so vastly modified from the ground plan of the order that little external evidence of relationship remains here. The frayed horny fringe is directed backward as a battery of barbs and the papillae of the posterior border are directed inward to permit withdrawal of the tongue within a skin sheath. The long hyoids of woodpeckers and the great extensibility of the tongue need no special description.

HORNY PALATE

The horny palate is in large measure dependent on the tongue and does not always provide direct evidence of relationship where adaptive re-arrangement has been extensive, as in the Picidae. In the other four families dissected there is a notable resemblance in the thin cutting edge of the tomium in the upper mandible, combined with the vaulting of the palate itself. This is so pronounced that little evidence of a lateral palate ridge, generally present in passerines, can be seen. The central ridge is strong in all families. Posterior palate relief is rather non-descript.

ECTETHMOID PLATE

The ectethmoid plate is convincingly similar in all of the piciform families and all have the foramen double. This condition is considered advanced in my work on the Oscines, primitive forms having a single foramen which is larger the more primitive they are. In Galliformes, a possible ancestor, the foramen may be said to occupy the entire plate which is not closed ventrally at all.

THE BILL

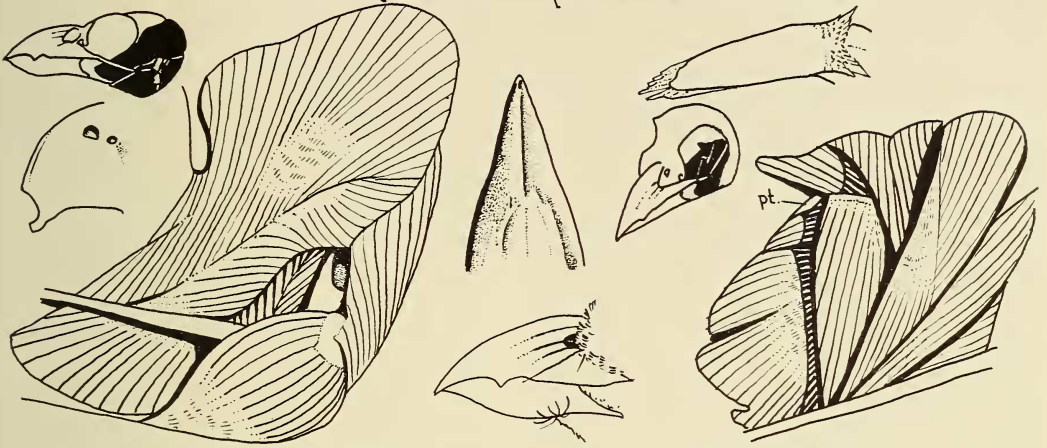
The bill is similar in ground plan in all but the woodpeckers and jacamars, with a very strongly bowed culmen and rather massive upper mandible. The nostril is far posterior, non-operculate and (in honeyguides) raised into a membranous tube. In barbets the bill may be long or short with the tomium sometimes notched as in *Lybius*, a feature that seems to be multiplied with length in the toucan bill. Barbets have abundant narial and chin bristles as do puffbirds, but the elongate, straightened bill of jacamars shows reduction of bristles. Puffbirds generally have narrowed, hooked bills. Toucans, woodpeckers, and honeyguides have the bristles virtually lacking and the bills without hooks, except for a slight tendency in toucans which are also much notched. The toucan bill is, of course, unique in the degree of lightness achieved with its cancellous internal structure.

In connection with the bill the barbets seem to be fruit and insect eaters, often expert flycatchers; puffbirds are lethargic flycatchers; jacamars, graceful and swift flycatchers. Toucans are fruit and insect eaters. Woodpeckers are specialized insect eaters, eating many wood-boring insects, but also anteaters and flycatchers, some taking sap and flower juices as well as fruit. Honeyguides are insect eaters that evidently have become specialized for eating honey and even getting nutrition out of beeswax. This adaptation will be discussed further.

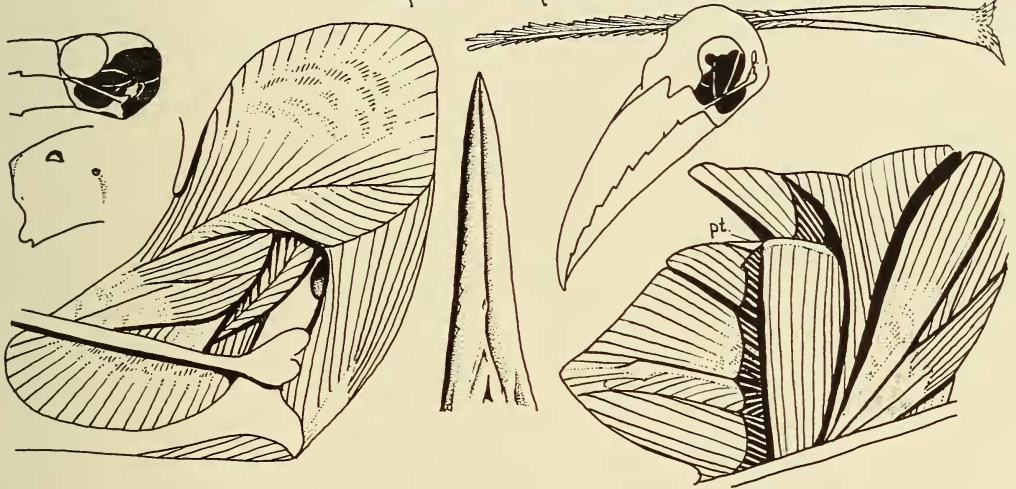
PLUMAGE

Barbets generally have brilliant plumage—barring and streaking on a ground of yellow or green with flashmarks of crimson—which is clearly similar to that of some woodpeckers. Puffbirds, with barred and streaked plumage also, are duller in color and jacamars are more often coppery green and iridescent brown in solid masses. The puffbirds *Nystalis* and *Malacoptila* (and the woodpecker, *Jynx*) resemble owls and nightjars in plumage, the jacamars resemble hummingbirds. This resemblance is not taken as evidence of direct relationship but other lines of evidence suggest that these orders and many others may be springing independently from Galliformes which I am inclined to regard as our most primitive, unspecialized bird stock. Toucans have plumage patterns of solid greens and yellows and reds suggestive of barbets. Honeyguides re-

BARBET ~ *Lybius leucocephalus* ~ CAPITONIDÆ



TOUCAN ~ *Pteroglossus torquatus* ~ RAMPHASTIDÆ



WOODPECKER ~ *Melanerpes erythrocephalus* ~ PICIDÆ

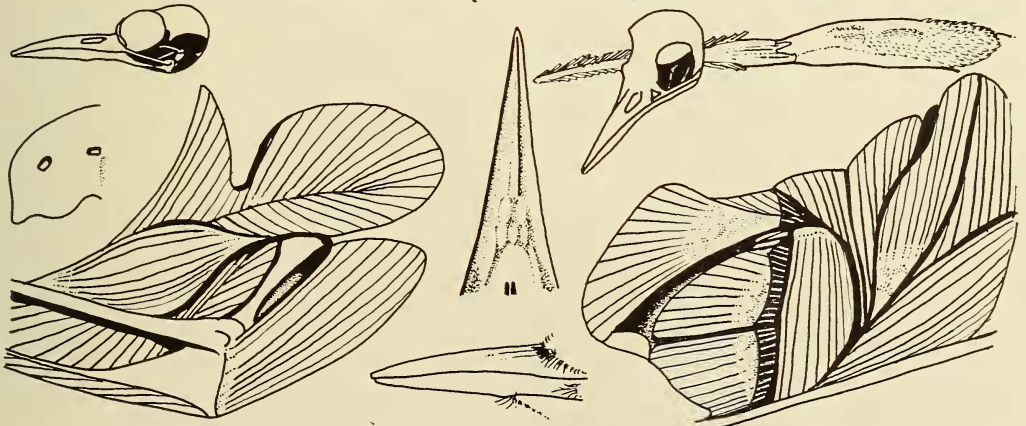


FIG. 2.—Detail drawing of jaw muscle pattern in the barbet (Capitonidae), toucan (Ramphastidae), and woodpecker (Picidae).

semble certain dull-patterned barbets like *Lybius leucocephalus*. On the basis of plumage, in fact, one would be inclined to say that all piciform families may have originated from the barbets. If so, it would have been before the bills became as specialized as they are now, in all probability.

OTHER CHARACTERS

The idea that the barbets may be the ancestral piciform family is supported by other characters which might be preadaptive to traits highly expressed in the other families. All these families have zygodactylous feet in which the second and third toes are directed forward, the first and fourth, backward. This arrangement of toes is particularly advantageous for birds climbing about on tree trunks as barbets and woodpeckers do or for perching. Toucans and honeyguides may have largely abandoned this trait without the toes being under any selection to return to the usual condition. Barbets have many of the woodpecking traits of Picidae with highly ossified interorbital septum, a feature found throughout the order, but especially in Picidae. Barbets excavate holes as do woodpeckers. Toucans nest in hollow trees. Honeyguides are parasitic on hole-nesting birds, often members of Piciformes, according to Bannerman (1933). In the pelvic appendage, the re-arrangement of the toes has resulted in changing the position of tendons and loss of the *ambiens* muscle, considered of important diagnostic value by Garrod (1873).

WAX-EATING IN THE HONEYGUIDES

As to the honey- and wax-eating adaptation in honey guides, no notable specialization of digestive organs was found. There is no sign of enlarged palatine salivary glands such as are found in all the nectar-eating groups of the world (Beecher, 1953)—Dicaeidae, Nectariniidae, Meliphagidae, and the New World hummingbirds and honeycreepers. If only honey were taken this would not be surprising because the bulk of this is immediately assimilable and there would be little need for invertase or any enzyme for breaking down sucrose. But Friedmann (MS.) has evidence that honeyguides are able to derive nutrition from beeswax, implying a rather complex enzyme action. With the specimens available I could carry out only the crudest sort of sampling technique aimed at studying wax digestion. I removed food material from the oral cavity, stomach, and hind gut of the species studied and

heated it on a scalpel blade. A wax residue was obtained on the blade from contents so treated of oral cavity and stomach of *I. exilis* and *I. maculatus* in some samples—never from the hind gut. This might suggest wax digestion in the stomach or small intestine were the sampling adequate. As it stands these results are merely suggestive.

This trait of the honeyguides is the more interesting because of their general flair for parasitism. They lay their eggs in the nests of other birds, often close relatives, and they have learned to get animals more capable than themselves to uncover the honey combs they prefer to feed on. They must have started this specialization in habit by leading animals, perhaps the honey badger (*Mellivora*) to hives. Chapin (1939) suspects other mammals, including squirrels and monkeys, of aiding the birds in getting at honey. The discovery, apparently only by *Indicator indicator*, that man could be led to bee trees with satisfactory results is necessarily a recent specialization of the trait.

SUMMARY AND CONCLUSIONS

An investigation of feeding adaptations in the head region of the piciform bird families, Capitonidae, Bucconidae, Ramphastidae, Picidae and Indicatoridae, was undertaken to study their morphological and systematic relationships. The jaw muscle pattern shows a strong facies resemblance in all, suggesting that the order Piciformes is a real unit. The honeyguides have the least specialized pattern and may represent the ground plan from which the other families have been derived, though other indications are that the barbets are nearer the ancestral stock. From this ground plan the barbets diverge by having more massive adductors and palatine retractors, the toucans by fusing the slips of *M. pterygoideus ventralis* and sheathing the musculature increasingly in aponeuroses for increased palate retraction. The woodpeckers extend enormously the origins of the mandibular protractors, particularly *M. protractor quadrati*, a powerful antagonist to the muscles of palate retraction, to produce a shock absorber for the bill. The tongue is so far modified in toucans and woodpeckers as to offer little positive evidence of relationship but the horny palate is less modified and the ectethmoid plate is similar in all. Bills and feeding habits suggest close but disjunct relationships in a single series and plumage suggests origin

of piciform families from the barbets or an ancestral group with a somewhat less-pronounced bill. Zygodactylous feet and the hole-nesting habit, taken in combination with the above, support present ornithological thought as to the unity of the order. The trait of honey guides of leading animals to bee hives seems to be part of a general parasitic complex which includes brood parasitism as well. No digestive abnormalities were noted but enzymes for wax digestion may be produced in stomach or small intestine.

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ZOOLOGY.—*Psammodesmus*, a neglected milliped genus (*Polydesmida*: *Platyrrhacidae*). RICHARD L. HOFFMAN, Clifton Forge, Va. (Communicated by H. F. Loomis.)

It is unfortunate that much of the previous work on diplopod taxonomy has been of rather poor quality. Far too often one finds himself obliged literally to revise a genus or tribe before feeling safe in placing an undescribed species. This is precisely the situation I encountered on endeavoring to place a new platyrrhacid milliped found in the collections of the U. S. National Museum. Fortunately, however, the problem has been of fairly easy resolution although depending upon some rather extensive nomenclatorial changes. Although the group directly involved is a South American one, it has been necessary to consider the entire family of the *Platyrrhacidae*. This has been made possible by the exceptionally useful treatise by Carl Attems, in *Das Tierreich*, Lief. 69, 1938. Despite the value of this reference, I believe that Attems's somewhat conservative treatment does not give proper recognition to the numerous species-groups whose characters seem clearly to be of generic level. Attems recognizes a single genus—divided into six subgenera—with the characters which I ascribe to the family *Platyrrhacidae*. (The other six genera of "*Platyrrhacidae*" treated in his monograph

are referable to the family *Euryuridae* in the sense of Pocock and Chamberlin.)

Interestingly enough, the first contribution to the systematics of the tropical American platyrrhacids, by O. F. Cook (1896), still appears to provide the most logical arrangement of the species! Cook was the first worker to break up the large widespread genus *Platyrrhacus* (*Acanthodesmus* or *Stenonia* of early writers) with the proposal of numerous generic names. His arrangement, although reasonable, was never generally accepted, and the most authoritative recent workers have reverted to the use of the name *Platyrrhacus* for the majority of the species. There are, however, within the family a great number of diverse types which, if they occurred in the temperate regions where faunas are better known, would long ago have been recognized as well-marked genera.

Cook's paper "New American *Platyrrhacidae*" (*Brandtia*, 1896, no. 12) included the diagnoses of nine new American genera. Four of these (*Nyssodesmus*, *Tirodesmus*, *Nanorrhacus*, and *Rhyphodesmus*) have been recognized at one time or another by American workers. Various others were accepted